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Paleomoropus, a New Early Eocene Chalicotherere (Mammalia, Perissodactyla), and a Revision of Eocene Chalicotheres

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INTRODUCTION

The discovery of a new early Wasatchian chalicotherere extends the known temporal range of the Chalicotherioidea back to the beginning of the Eocene and provides new evidence concerning the early radiation of the Perissodactyla. A study of all North American, European, and Asiatic Eocene chalicotheres has resulted in several basic taxonomic changes and a new interpretation of the early deployment of the Chalicotherioidea.

I wish to thank Prof. Glenn L. Jepsen of Princeton University for generously allowing me to describe the type of *Paleomoropus*; Dr. C. L. Gazin, United States National Museum, Smithsonian Institution, and Mr. William D. Turnbull, Chicago Natural History Museum, for the loan of specimens in their collections; and Dr. Otto Zdansky for providing casts and photographs of Asiatic chalicotheres in the collections of the Paleontological Institute, the University of Uppsala, Sweden. Drs. Donald E. Russell and Donald E. Savage provided useful information on European chalicotheres, and Dr. Malcolm C. McKenna read the manuscript and offered helpful suggestions. Dr. Mary Dawson kindly provided the photograph of a Carnegie Museum specimen reproduced

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in figure 2. Mr. Chester Tarka prepared the stereophotograph shown in figure 1. The present investigation was carried out during the tenure of a National Science Foundation Postdoctoral Fellowship in the Department of Vertebrate Paleontology of the American Museum of Natural History.

ABBREVIATIONS

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum, Pittsburgh, Pennsylvania
C.N.H.M., Chicago Natural History Museum, Chicago, Illinois
G.M.P., Geological Museum, Peking, China
P.U., Princeton University, Princeton, New Jersey
U.C.M.P., University of California Museum of Paleontology, Berkeley, California
U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D.C.

ORDER PERISSODACTYLA OWEN, 1848

SUBORDER ANCYLOPODA COPE, 1889

SUPERFAMILY CHALICOTHERIOIDEA GILL, 1872

FAMILY EOMOROPIDAE MATTHEW, 1929

PALEOMOROPUS,¹ NEW GENUS

TYPE: *Paleomoropus jepsoni*, new species.

KNOWN DISTRIBUTION: Early Eocene of North America.

DIAGNOSIS: Small chalicotheres with very low-crowned teeth. Ectoloph of upper molars relatively narrow and undeveloped, with small parastyle (compared to later chalicotheres) and no mesostyle. Transverse lophs relatively long, with protoconule and protocone aligned along protoloph and not deflected posteriorly. Last lower molar with large hypoconulid.

***Paleomoropus jepsoni*,² new species**

Figure 1

TYPE: P.U. No. 13254, left M¹ and M³, right M².

HYPODIGM: Type only.

HORIZON AND LOCALITY: Lower Gray Bull beds (= early Wasatchian or very early Eocene), Willwood Formation, Sand Coulee Basin, sect. 9, T. 55 N., R. 102 W., Park County, Wyoming.

¹ *Paleo*, old, plus *Moropus*; an ancestor of *Moropus*.

² Named in honor of Prof. Glenn L. Jepsen, whose diligent field work led to the discovery of this and many other unique specimens.

DIAGNOSIS: Sole known species of genus. Length-width measurements of upper molars as follows: M^1 , approximately 14.0 mm. long; M^2 , 14.0 mm. long and 16.0 mm. wide; M^3 , 15.6 mm. long and 18.0 mm. wide. Length of M^{1-3} , approximately 44 mm.

DESCRIPTION: (See fig. 1). M^1 is heavily worn and lacks the anterolabial corner; M^2 and M^3 are complete and progressively less worn. The basic molar cusp pattern is as follows: parastyle large and anterolabially displaced; paracone sharply conical, with thin anterior and posterior ridges

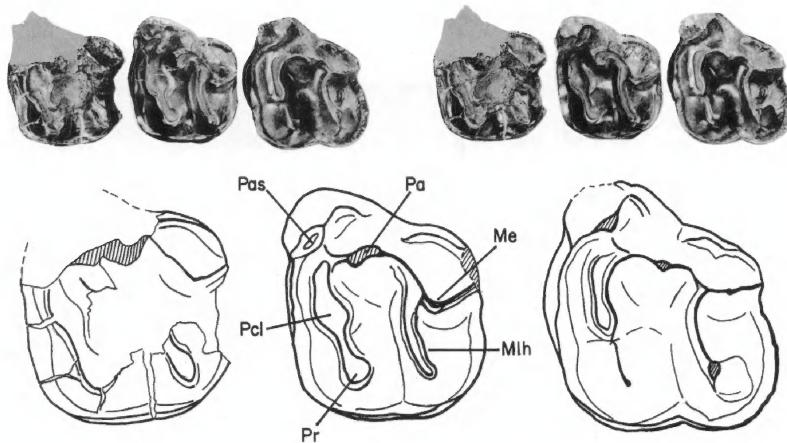


FIG. 1. *Paleomoropus jepseni*, new genus and species, type, P.U. No. 13254, occlusal view of left M^{1-3} (M^2 reversed). Above: Stereophotograph. Natural size. Below: Interpretive drawing. $\times 2$.

Abbreviations: Me, metacone; Mlh, metaloph; Pa, paracone; Pas, parastyle; Pcl, protoconule; Pr, protocone.

(to protoloph and metacone, respectively); no mesostyle; metacone lingually displaced and slightly convex labially; protoloph with symmetrical medial bulge, followed lingually by a sharp constriction (on both anterior and posterior sides), which delimits a lophoid protoconule; lingual half of protoloph straight, protocone not deflected posteriorly; metaloph high and uninterrupted (no metaconule), terminating high at the ectoloph; basal cingula on anterior, lingual, posterior, and postero-labial sides. M^3 differs from M^1 and M^2 in being larger and having a larger and more labially displaced parastyle and a slightly shorter metacone. A large wear facet on the posterior side of the M^3 hypocone (lingual end of the metaloph) indicates that M_3 had a large hypoconulid.

DISCUSSION: *Paleomoropus jepseni* is assigned to the Chalicotherioidea

because it possesses a distinct protoconule on the protoloph and a high, uninterrupted metaloph, a combination of molar cusp features found only in that superfamily. In equoids the metaloph is interrupted by a metaconule and is low at the ectoloph; in brontotherioids there is no posterior shearing loph, only a large isolated hypocone; in tapiroids and rhinocerotoids both protoloph and metaloph are high, continuous shearing lophs, uninterrupted by intermediate cuspules.¹ In addition, the large parastyle of *Paleomoropus* is characteristic of, though not confined to, chalicotheres.

The absence of a mesostyle in such an early chalicothere as *Paleomoropus* is not surprising, for the oldest known equoid, *Hyracotherium*, also lacks a mesostyle, a feature presumably not present in the ancestral stem perissodactyl. In addition, *Lophiaspis*, an early Eocene genus here transferred to the Chalicotherioidea, lacks a mesostyle, as does *Litolophus gobiensis*, an Asiatic late Eocene chalicothere described below in this paper. A molar mesostyle occurs in all chalicotheres only after the beginning of the Oligocene.

Paleomoropus jepseni can be distinguished from all later chalicotheres by the characteristics listed in the generic diagnosis. Knowledge of the complete dentition should reveal further differences, which will probably include less molariform premolars, larger hypoconulid on M_3 , and less prominent, less lingually directed lower molar metalophids than in later chalicotheres. *Paleomoropus* most closely resembles the European genus *Lophiaspis*, from which it differs in having a bilaterally symmetrical, not posteriorly deflected, protoconule, a less posteriorly extended protocone, and lower, more obtuse, lophs. Among North American early Eocene perissodactyls, *P. jepseni* is most similar to the tapiroid *Heptodon posticus*, from which it can be distinguished by the distinct protoconule and, less importantly, the larger parastyle.

TAXONOMIC IMPLICATIONS: At present the order Perissodactyla is divided into two suborders on the basis of molar cusp pattern: the Hippomorpha, comprised of equoids, brontotherioids, and chalicotherioids, and the Ceratomorpha, comprised of tapiroids and rhinocerotoids (Wood, 1934, p. 260; 1937, p. 106; Simpson, 1945). Hippomorphs are characterized by the presence of W-shaped ectolophs (due to the development of a mesostyle) on the upper molars and oblique metalophids on the lowers,

¹ Some specimens of the oldest known tapiroid, *Homogalax*, exhibit a barely distinct protoconule on the protoloph, but this is accompanied by a corresponding metaconule on the metaloph and is a variable last vestige of an ancestral feature never seen in later tapiroids. The European genus *Lophiaspis*, formerly considered a tapiroid with a molar protoconule, is in this paper assigned to the Chalicotherioidea.

while in ceratomorphs the ectoloph is straight, lacking a mesostyle, and the metalophid, when present, extends anteriorly. However, the molars of *Paleomoropus jepseni* reveal that when chalicotheres diverged from other hippomorphs they lacked mesostyles and, presumably, since the two are correlated, oblique metalophids. Thus the molar cusp pattern considered diagnostic of the Hippomorpha must have evolved independently in at least two (and possibly all three) hippomorph superfamilies. This raises the question of whether chalicotheres should actually be associated with equoids and brontotherioids in the suborder Hippomorpha.

Except for the occurrence of W-shaped ectolophs and oblique metalophids in advanced chalicotherere molars, the basic molar pattern of chalicotherioids is quite different from that of other hippomorphs. In equoids both anterior and posterior upper molar cross lophs are interrupted by intermediate cuspules, and the metaloph is low at the ectoloph; in brontotherioids the metaconule was lost, leaving the hypocone as a large isolated cusp. The presence of intermediate cuspules is a hold-over from the primitive sextubercular molar pattern of the condylarth ancestors of the Perissodactyla. In chalicotheres, on the other hand, although a protoconule is retained on the protoloph, the metaconule is completely merged into the metaloph, which, even in the earliest Eocene genus *Paleomoropus*, is a high, unbroken, shearing crest. This is an advanced modification never attained in other hippomorphs, but characteristic of ceratomorphs (in which, however, the anterior row of cusps was also converted into an unbroken shearing crest). Resemblance to tapiroids is most striking in the earliest chalicotheres, which have relatively narrow and undeveloped ectolophs and long transverse shearing lophs (compare *Paleomoropus* with *Heptodon*). However, in later chalicotheres, the development of a mesostyle and relative enlargement of the ectoloph (coincident with emphasis in mastication on vertical ectoloph shear) overshadow the more lingual cusp features and result in close resemblance to the molar pattern of equoids and, even more closely, that of brontotherioids. Thus it seems likely that convergence (in development of a W-shaped ectoloph and, concomitantly, oblique metalophid) and parallel retention of primitive features (distinct protoconule) have resulted in a misleading similarity between the molar pattern of advanced chalicotherioids and that of equoids and brontotherioids. The basic chalicotherere molar pattern is actually no more similar to that of other hippomorphs than it is to the ceratomorph molar pattern.

Additional evidence of the uniqueness of chalicotherioids, besides the molar pattern, is seen in the development of clawed unguals in advanced chalicotheres. This feature, which occurs in no other group of perissodactyls, led early workers to consider the chalicotheres (then known

primarily from the late Tertiary) a separate order (Ancylopoda Cope, 1889).

The early age of *Paleomoropus* further suggests a long independent evolutionary history for the Chalicotherioidea. *Paleomoropus* occurs approximately contemporaneously with the oldest known equoid (*Hyracotherium angustidens*) and tapiroid (unnamed species of *Homogalax*) from the earliest Eocene Four Mile fauna of northern Colorado (McKenna, 1960, p. 119; Radinsky, 1963a, p. 17). These latter two forms are extremely similar, which suggests that equoids and tapiroids separated not long before the beginning of the Eocene. Since *Paleomoropus* was already distinctly a chalicotherioid by that time, it would appear that chalicotheres diverged from the basic perissodactyl stock before the equoid-tapiroid split.

Thus, on the basis of morphological and chronological evidence, chalicotheres appear to be as different from other hippomorphs as from ceratomorphs. Such difference was suggested by Scott (*in* Scott and Jepsen, 1941, p. 747) when he placed the superfamily Chalicotherioidea in a separate suborder, Ancylopoda (new rank for the Order Ancylopoda Cope, 1889), and ranked the Ceratomorpha and Hippomorpha (*sensu stricto*) as major subdivisions of a new suborder, Chelopoda (hoofed foot). However, that arrangement implies that equoids and brontotherioids are more similar to tapiroids and rhinocerotoids than either group is to chalicotherioids. Although this is suggested by the similarity between equoids and tapiroids in earliest Eocene time, I do not think that the evidence is at present definite enough to warrant formal taxonomic expression. Until more is known about the relationships between perissodactyl superfamilies in early Eocene time, I suggest that the Hippomorpha (*sensu stricto*) and Ceratomorpha be kept at subordinal rank and that the Ancylopoda be added as a third suborder. The major subdivisions of the Perissodactyla would then be as follows:

Order Perissodactyla
Suborder Hippomorpha
 Superfamily Equoidea
 Superfamily Brontotherioidea
Suborder Ceratomorpha
 Superfamily Tapiridea
 Superfamily Rhinocerotoidea
Suborder Ancylopoda
 Superfamily Chalicotherioidea

It should be noted here that, while rhinocerotoids were probably derived from an early Eocene tapiroid (such as *Heptodon*), the relationship between equoids and brontotherioids is by no means so clear. The most primitive known brontotherioid, *Lambdotherium*, first appears late in the

early Eocene, already quite distinct from the contemporary equoid, *Hyracotherium*. Nothing in the known anatomy of *Hyracotherium* precludes its being ancestral to *Lambdotherium*, but the morphological gap between those two genera is greater than that between ancestral tapiroid and primitive rhinocerotoid, and intermediate stages are not known. When details of the origin of brontotheroids become known, the classification proposed above may have to be further modified to dissociate brontotheroids from equoids. Should such separation become necessary, it would probably be best to drop the subordinal divisions of the Perissodactyla and leave the order divided into five superfamilies.

REVISION OF EOCENE CHALICOOTHERES

Chalicotherioid remains are rare in Eocene beds, and most of the named genera and species are known from very few specimens. Nevertheless, a re-examination of all Eocene chalicotheres species has revealed a hitherto unsuspected diversity of forms, which necessitates basic taxonomic changes and reveals a new picture of the early evolution of the Chalicotherioidea. All Eocene chalicotheres are placed in the family Eomoropidae, characterized as follows:

FAMILY EOMOROPIDAE MATTHEW, 1929¹

REVISED DIAGNOSIS: Primitive, small to medium-sized chalicotheres with low-crowned teeth. Upper and lower canines medium-sized to greatly enlarged. First upper premolar present, in some cases separated from the second by a diastema. Premolars submolariform; premolar series long relative to molars. Upper molars relatively wide, with prominent transverse lophs and relatively narrow, undeveloped ectolophs; molar parastyles isolated, mesostyles absent to small, and protocones more or less in line with protoloph. Lower molar metalophids terminate labial to the metastylid; last lower molar with hypoconulid. Auditory bulla relatively smaller than in later chalicotheres. Manus tetradactyl, pes tridactyl; digits not sharply flexed, condition of unguals unknown.

PALEOMOROPUS, NEW GENUS (DESCRIBED ABOVE)

LOPHIASPIS DEPÉRET, 1910

TYPE SPECIES: *Lophiaspis maurettei* Depéret, 1910.

¹ Proposed as a subfamily by Matthew (1929, p. 519); raised to family rank by Viret (1958, p. 417).

DISTRIBUTION: Early to middle Eocene of Europe.

REVISED DIAGNOSIS: Upper molars similar to those of *Paleomoropus* but with higher and sharper lophs, posteriorly deflected protoconules, and more posteriorly extended protocones. C^1 medium-sized. P^1 not present immediately anterior to P^2 .

DISCUSSION: Depéret (1910, p. 559) erected the genus *Lophiaspis* for a line of European tapiroid-like forms which differ from *Lophiodon* mainly in the presence of a distinct protoconule on the protoloph. From Depéret's illustration of the type species, *Lophiaspis maurettei* (1910, pl. 7, fig. 1), it appears that *Lophiaspis* may also differ from *Lophiodon* in having relatively larger molar parastyles. Until now *Lophiaspis* has been classified as a lophiodontid tapiroid, but, on the basis of the distinct protoconule on the protoloph, coupled with a high, uninterrupted metaloph and, less important, the large parastyle, I suggest that *Lophiaspis*, like *Paleomoropus*, is actually a primitive chalicotheres (see discussion on p. 4).

Lophiaspis is more advanced than the North American genus *Paleomoropus* in having higher and more acute lophs, a posteriorly deflected protoconule, and a more posteriorly extended protocone. *Lophiaspis* differs from the late Eocene chalicotheres *Eomoropus* in having a more broadly convex, less lingually depressed paracone and in lacking a mesostyle. Depéret (1910, p. 560) stated that *Lophiaspis maurettei* lacked P^1 ; from his illustration (pl. 7, fig. 1), it is apparent that P^1 was not present immediately anterior to P^2 , but not enough of the postcanine diastema is shown to reveal whether or not P^1 was present between P^2 and C^1 , as in some later chalicotheres. Absence of P^1 would remove *Lophiaspis* from the ancestry of all known late Eocene chalicotheres.

The type of *Lophiaspis maurettei* was found near Palette, Aix-en-Provence, France, at the base of a lacustrine limestone sequence containing non-marine mollusks of Lutetian (middle Eocene) age, overlying beds with Sparnacian (early Eocene) mollusks. On the basis of a diminutive equoid associated with the *Lophiaspis* remains, D. E. Savage (personal communication) suggests that the Palette mammalian fauna is probably of Lutetian age.

An isolated upper molar in the collections of the University of California Museum of Paleontology (U.C.M.P. No. 63667) appears identical to M^1 or M^2 of *Lophiaspis maurettei* and comes from beds of Sparnacian age at Mutigny, Marne, France.

Besides *L. maurettei*, Depéret (1910, pp. 561-562) assigned two later species, *L. baicheri* (of middle Lutetian age) and *L. occitanicus* (of late Lutetian age) to *Lophiaspis*. From his illustrations (pl. 7, figs. 2-3) these later forms do not appear to have so prominent a protoconule as does

the type species, and perhaps should more properly be assigned to the tapiroid genus *Lophiodon*. However, the illustrations alone are inadequate for a specific revision of *Lophiaspis*; this should be done only after a first-hand examination of the pertinent specimens in European museums.

EOMOROPUS OSBORN, 1913

TYPE SPECIES: *Eomoropus amarorum* (Cope), 1881.

DISTRIBUTION: Late Eocene of North America and Asia.

REVISED DIAGNOSIS: Small, lightly built chalicotheres with low-crowned teeth. Presence or absence of upper canine and first premolar not definitely known. Upper molars slightly wider than long, with moderately large, isolated parastyles, small mesostyles, and slightly lingually depressed paracones; protoconules and, to a lesser degree, protocones deflected posteriorly. Mandible relatively long and slender, with a long shallow symphysis and low ascending ramus. All lower incisors present, followed immediately by a medium-sized canine; postcanine diastema relatively long. P^1 absent. Lower molar metalophids not so lingually directed as in later chalicotheres, terminating low at the protolophid, between protoconid and metaconid; metastylids prominent. M_3 with small hypoconulid.

DISCUSSION: Osborn (1913, p. 262) noted that *Triplopus amarorum* Cope, 1881, is a chalicotherioid, not a rhinocerotoid, and therefore made it the type of a new genus, *Eomoropus*. The upper molars of *Eomoropus* differ from those of the early Eocene *Paleomoropus* in the following features: lophs higher and sharper; ectoloph more prominent, with a mesostyle developed, paracone more lingually depressed and less convex, and parastyle relatively larger; protoconule, and to a lesser degree protocone, posteriorly deflected. Knowledge of the rest of the dentition of *Paleomoropus* will probably reveal additional differences which, judging from evolutionary trends observed in other groups of Eocene perissodactyls, should include an increase in the premolar molarization and a reduction in size of the M_3 hypoconulid in *Eomoropus*.

Eomoropus differs from Oligocene and later chalicotheres in the following features: smaller and more lightly built, with feet unspecialized (digits not sharply flexed); premolar series longer relative to molars; upper molars relatively wider and ectolophs less prominent relative to cross lophs, with paracone less lingually depressed, especially on M^3 , mesostyle smaller, and parastyle separated from rest of ectoloph; protocone less posteriorly deflected; P_{3-4} less molariform (metalophid less lingually directed); M_{1-3} with prominent metastylids and metalophids low and not so lingually directed; M_3 retaining small hypoconulid.

Oligocene and later chalicotheres lack C^1 and P^1 . No known North American specimens of *Eomoropus* preserve the maxilla anterior to P^2 , but an isolated maxillary fragment probably belonging to the Asiatic species *Eomoropus quadridentatus* Zdansky, 1930, shows a double-rooted alveolus immediately anterior to P^2 (Zdansky, 1930, pl. 4, figs. 11-12). If P^1 was present in *Eomoropus amarorum*, it probably was not situated immediately adjacent to P^2 , because there is no evidence of wear on the anterior slope of P_2 ; it may have been present a short distance anterior to P^2 as in other genera of late Eocene chalicotheres. In short, there is no reason to believe that C^1 and P^1 were lost in *Eomoropus*, and there is some evidence that suggests that P^1 was present at least in one species of that genus.

Eomoropus amarorum (Cope), 1881

Figure 2

Triplopus amarorum COPE, 1881, p. 389.

Eomoropus annectens PETERSON, 1919, p. 139.

TYPE: A.M.N.H. No. 5096, cranial portion of a skull, with M^2 roots and lingual half of M^3 the only upper dentition preserved, lower jaw with I_{1-3} and C_1 roots, and P_2-M_3 , three cervical vertebrae, manus and pes lacking phalanges, tibia, and incomplete pelvis and femur. (Figured in Cope, 1884, pl. 55a, figs. 6-9, pl. 58a, fig. 2, and in Osborn, 1913, figs. 1, 3-8.)

HORIZON AND LOCALITY: Early late Eocene Washakie B beds (= Uinta B), Washakie Basin, Wyoming.

REFERRED SPECIMENS: C.N.H.M. No. P.M.1670, P_4-M_3 , from Washakie B beds, Washakie Basin; C.M. No. 3109, the type of *Eomoropus annectens*, maxilla, with P^2-M^3 and postglenoid process, from early late Eocene Uinta B beds, Uinta Basin, Utah; P.U. No. 18067, M^{2-3} lacking parastylar region, from Uinta B beds, Uinta Basin.

DIAGNOSIS: P^1 unknown, probably not situated immediately anterior to P^2 . Lower premolars slightly less molariform than those of *Eomoropus quadridentatus*. Length of M_{1-3} , 53 mm., of P_{2-4} , 33 mm. (A.M.N.H. No. 5096); length of M^{1-3} , 46 mm., of P^{2-4} , 29 mm. (C.M. No. 3109).

DISCUSSION: Peterson (1919, p. 139) distinguished *Eomoropus annectens* from *E. amarorum* by the following features: skull of *E. annectens* narrower across orbit and palate (measured from internal face of M^3 to lower external border of jugal), longer in cranial region (measured from M^3 to postglenoid process), less abruptly contracted laterally in orbital region, postglenoid process lighter, and smaller size. However, comparing the type of *E. annectens*, C.M. No. 3109 (figured in Peterson, 1919, pl. 36,

fig. 2), with that of *E. amarorum*, I find no evidence for the first four differences; the distance from the internal face of M^3 to the lower external border of the jugal is about 30 mm. in both specimens, the distance from M^3 to the postglenoid process measures about 58 mm. in both, slight distortion due to lateral crushing in the type of *E. amarorum* accounts for the third difference, and, finally, the postglenoid process of *E. annectens* does not appear smaller than that of *E. amarorum*. The upper dentition of *E. annectens* is a little too small (by about 7%) to occlude with the lower dentition of the type of *E. amarorum*, but the difference does not seem to me significant enough to justify maintaining *Eomoropus annectens* as a separate species. For these reasons I place *E. annectens* in synonymy with *E. amarorum*.

Upper and lower dentitions of *Eomoropus amarorum* are illustrated in figure 2 and need no further comment here. A.M.N.H. No. 5096, the best-preserved skull of an Eocene chalicotheres, has been described in detail by Cope (1881, pp. 389-391; 1884, pp. 687-689) and less thoroughly by Osborn (1913, p. 268), although Osborn's (p. 262, fig. 1) illustrations are the best ones extant. As in later chalicotheres, the tympanic of *Eomoropus* is expanded laterally to form a flat ventral floor to the external auditory meatus, and anteromedially as a long, thin, vertical ridge. There is, however, no expansion of the entotympanic into a large inflated bulla, as is seen in the Miocene chalicotheres *Moropus*; the narrow convex strip of bone exposed between tympanic and basioccipital in *E. amarorum*, identified as petrosal by Cope and Osborn, may be the entotympanic (also suggested by van der Klaauw, 1931, p. 323). The foramen ovale is separated by a wide strip of sphenoid from the middle lacerate foramen (which is quite narrow in *Eomoropus*), and there is a short alisphenoid canal; these are primitive perissodactyl features which persist in later chalicotheres. An unusual feature in the skull of *Eomoropus* is a very prominent, sharp-edged ridge which extends anterodorsally immediately above the sphenorbital and optic foramina, terminating a short distance below the posterior border of the supraorbital process. A less prominent version of this ridge occurs in *Moropus*. Finally, the frontals are expanded as a broad flat table above the orbits, terminating laterally in prominent supraorbital processes, which are pierced by the supraorbital foramina.

The mandible of *Eomoropus amarorum* (see Osborn, 1913, p. 267, fig. 3) is relatively long and slender, with a long shallow symphysis, a prominent posteriorly projecting angular process (which extends farther back than is apparent in Osborn's figure), and an unusually low condyle. In *Moropus* the condyle is relatively higher and the angular process more broadly convex and less posteriorly projecting.

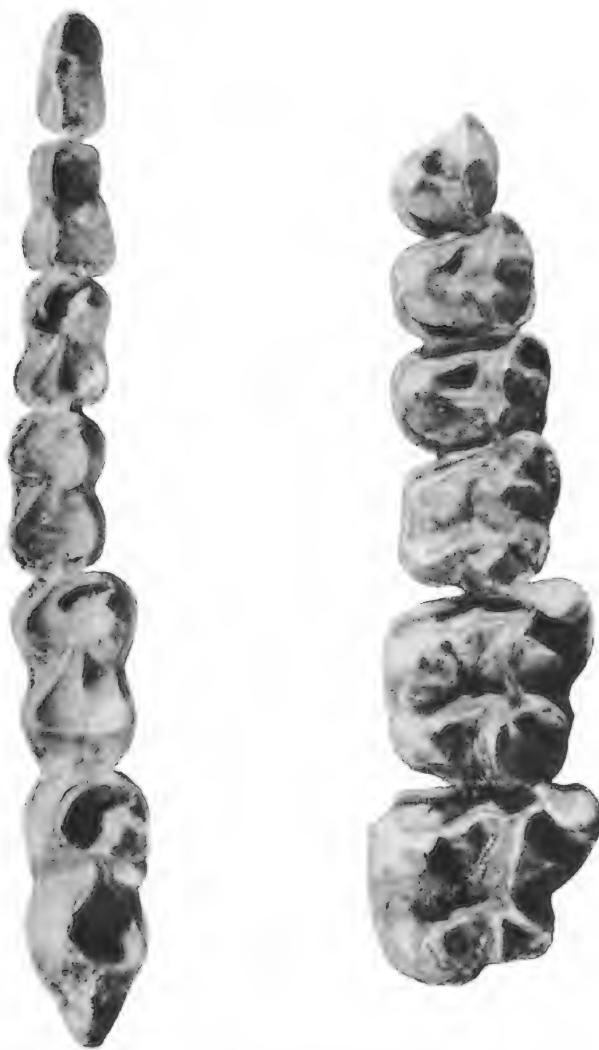


FIG. 2. *Eomoropus amarorum*, occlusal view of upper and lower cheek teeth. *Left*: A.M.N.H. No. 5096, left P_2 - M_3 . *Right*: C.M. No. 3109, left P^2 - M^3 . Both $\times 1.5$.

Osborn (1913, pp. 269-270, figs. 4-5) described and figured the manus and pes of *Eomoropus amarorum* preserved in A.M.N.H. No. 5096. The four-toed manus is complete except for the trapezium and phalanges and resembles that of other Eocene perissodactyls of about the same size, such as *Hyracoides*. The carpals are relatively somewhat shorter, and the

metacarpals are noticeably shorter, than those of cursorial Eocene equoids and helaletid tapiroids, which suggests that *Eomoropus* was not particularly specialized for running. Osborn (1913, p. 269) stated that the distal ends of the metacarpals of *Eomoropus* resembled those of *Moropus*, with discontinuous sesamoidal and phalangeal facets indicating the peculiar chalicotherid specialization of clawed unguals. In *Moropus* metacarpals the sesamoidal facet is relatively long and flat, with a low keel, and is oriented at a sharp angle to the short, convex, phalangeal facet. The metacarpals of *Eomoropus*, however, have approximately equal-sized, fairly continuous, evenly convex sesamoidal and phalangeal facets, with a high keel on the sesamoidal facet, as in other Eocene perissodactyls. There is no evidence that the feet of *Eomoropus* had clawed unguals.

The pes of *Eomoropus amarorum* preserved in A.M.N.H. No. 5096 includes a complete tarsus and proximal halves of the three metatarsals. The tarsus resembles that of a relatively unspecialized Eocene perissodactyl, such as *Hydrachnus*, except that the navicular and cuboid are slightly relatively shorter and wider. The astragalus has a long neck and relatively deep and narrow trochlea, unlike astragali of later chalicotheres. Osborn (1913, p. 270) erred in stating that in *Eomoropus* the navicular joined the calcaneum and widely separated the astragalus from the cuboid, as in schizotherine chalicotheres. In *Eomoropus* the navicular touches the calcaneum only for a short distance in front, and posteriorly (not visible in anterior view) there is still an extensive astragalus-cuboid contact. This condition is similar to that in the primitive tapiroid *Heptodon* and cannot be considered a distinctive chalicotherioid feature. In short, I can find no features in the manus or pes of *Eomoropus* which suggest in any way the extraordinary modifications which appear in the feet of later chalicotheres.

Eomoropus quadridentatus Zdansky, 1930

Eomoropus? *quadridentatus* ZDANSKY, 1930, p. 62.

TYPE¹ AND HYPODIGHM: Several incomplete dentitions, including all cheek teeth except P^1 and P^3 , in the collections of the Paleontological Institute of the University of Uppsala, Sweden. (Figured in Zdansky, 1930, pl. 3, figs. 24-25, pl. 4, figs. 9-14.)

¹ Zdansky failed to designate a type specimen for *E. quadridentatus*, and I am not aware of any such designation by a subsequent reviewer. If this is correct, the species is without a type. To rectify this situation, I select the maxilla with P^4 - M^3 , figured in Zdansky (1930, pl. 4, figs. 9-10), to be the type of *Eomoropus quadridentatus*.

HORIZON AND LOCALITY: Late Eocene beds in northern Honan, China.

DIAGNOSIS: About the same size as *Eomoropus amarorum*, but with slightly more molariform premolars and P^1 probably present immediately anterior to P^2 .

DISCUSSION: The premolar and molar cusp patterns of *Eomoropus quadridentatus* appear similar enough to those of *E. amarorum* to warrant definite assignment of *quadridentatus* to *Eomoropus*. Differences noted between the two species include the following: *E. quadridentatus* P_2 with posterolingual ridge (according to Zdansky, 1930, p. 64, but not discernible in his pl. 4, fig. 14); P_3 with higher paraconid; P_4 with shorter trigonid; P^1 present immediately anterior to P^2 , and P^2 with more prominent metacone. The association of the maxillary fragment preserving P^1 roots and P^2 with the other specimens of *Eomoropus quadridentatus* is probably correct, for the P^2 is similar in size and cusp pattern to that tooth in *E. amarorum* (differing only in having a slightly larger metacone).

Zdansky (1930, pp. 66-67) named two additional species of *Eomoropus*, each based on a single tooth, from the same locality as *E. quadridentatus*. *Eomoropus?* *minor* (*ibid.*, pl. 5, figs. 3-4) is based on an upper molar which is about 40 per cent smaller than M^1 in *E. quadridentatus* and has the proportions of a deciduous tooth (longer than wide). If the type and sole specimen of *E.?* *minor* is a deciduous tooth, it may represent the same species as *E. quadridentatus*.

The second species, *Eomoropus?* *major*, is here provisionally assigned to *Grangeria* (see below, p. 17).

GRANGERIA ZDANSKY, 1930

TYPE SPECIES: *Grangeria canina* Zdansky, 1930.

DISTRIBUTION: Late Eocene of Asia and ? North America.

DIAGNOSIS: Small to medium-sized chalicotheres, with low-crowned teeth. P_1 absent. Lower cheek teeth similar to those of *Eomoropus*, but canines disproportionately larger, mandible relatively deeper, and symphysis short.

DISCUSSION: The relatively large canines and deep mandible with truncated symphysis mark a major specialization which separates *Grangeria* from *Eomoropus* and furthermore removes *Grangeria* from the ancestry of all later chalicotheres (which have long shallow jaws, no upper canines, and small lower ones). The lower cheek teeth and apparently also the upper premolars of *Grangeria* are basically similar to those of *Eomoropus*, with a few minor differences noted below. Unfortunately the upper

molars of *Grangeria canina* are unknown; upper molars of a related species, *G.?* *anarsius*, differ from those of *Eomoropus* in having relatively larger parastyles.

Grangeria gobiensis Colbert, 1934, is here removed from *Grangeria* and made the type of a new genus, for reasons discussed below.

Grangeria canina Zdansky, 1930

TYPE: Maxillary fragments with P^1-3 and P^4-M^3 roots, mandibular fragments with C_1 , P_2-M_2 , and M_3 alveolus, all presumably from one individual, in the collections of the Paleontological Institute of the University of Uppsala, Sweden. (Figured in Zdansky, 1930, pl. 4, figs. 15-16, pl. 5, figs. 5-12.)

HORIZON AND LOCALITY: ? Late Eocene beds, Shantung, China.

DIAGNOSIS: Size large: length of M^{1-3} , about 64 mm.; length of M_{1-3} , 70 mm. P^1 present a short distance anterior to P^2 ; P^2 relatively large, with small, posteriorly displaced protocone.

DISCUSSION: The dentition of *Grangeria canina* has been described in detail by Zdansky (1930, pp. 67-71). The following remarks will concern only the more important features, as interpreted from Zdansky's illustrations (cited above).

The first upper premolar (P^1) is a single-cusped, labiolingually compressed tooth situated a short distance (4 mm. in the type) anterior to P^2 . The second upper premolar (P^2) is relatively longer and has a smaller and more posteriorly displaced protocone than P^2 of *Eomoropus*. In *Grangeria*, P^2 and apparently also P^1 are larger relative to the following cheek teeth than are P^2 and P^1 in *Eomoropus*, possibly owing to fringe effects of the growth field of the presumably hypertrophied upper canine. However, the lower anterior premolars of *G. canina* do not appear to be relatively enlarged (judging from Zdansky's size estimates).

The lower canine in *Grangeria canina* is a greatly enlarged curved tusk, projecting over 35 mm. from the base of the enamel (height estimated by Zdansky, 1930, p. 70; see his illustrations, p. 70, fig. 5, and pl. 5, fig. 10). This is in marked contrast to the lower canine in *Eomoropus amarorum* which, judged from the roots preserved in A.M.N.H. No. 5096, was a considerably smaller tooth, not enlarged over the primitive perissodactyl condition. In post-Eocene chalicotheres the lower canine becomes relatively even smaller than that in *Eomoropus*.

Probably to accommodate the enlarged lower canine, the mandible of *Grangeria canina* is relatively much deeper, and the symphysis is deeper and shorter, than in *Eomoropus*. In *G. canina* the ratio of ramus depth

(below anterior of M_3) to length of M_{1-3} is about 0.75; in *E. amarorum* the same ratio equals 0.62.

An additional difference in mandible structure, judged from the fragment figured in Zdansky (1930, pl. 4, fig. 15), is that the angular process in *G. canina* projected relatively more downward (below the ventral border of the horizontal ramus) than in *Eomoropus* or later chalicotheres.

The lower cheek teeth (P_2-M_2) are similar in cusp pattern to those of *Eomoropus*; from Zdansky's illustrations, the M_{1-2} metalophids appear to be slightly more oblique than those in *E. amarorum*. The M_3 alveolus indicates a hypoconulid similar to that of *Eomoropus*.

The age of *Grangeria canina* is open to question, since no other diagnostic fossils were found with it. *Grangeria canina* appears to be most closely related to *G. anarsius* from the late Uintan of North America (discussed below) and therefore is tentatively assigned a late Eocene age. In view of its larger size, *G. canina* may be slightly younger than *G. anarsius*, although this evidence is far from conclusive.

Grangeria? anarsius (Gazin), 1956, new combination

Eomoropus anarsius GAZIN, 1956, p. 12.

TYPE AND SOLE SPECIMEN: U.S.N.M. No. 21097, most of left side of skull, with C^1 , P^3 , and M^{1-3} , mandible with P_2 roots and P_3-M_3 . (Figured in Gazin, 1956, pl. 2, figs. 1-3.)

HORIZON AND LOCALITY: Late Eocene Badwater fauna (= Uinta C), Hendry Ranch Member of the Tepee Trail Formation, SE. $\frac{1}{4}$, sect. 9, T. 39 N., R. 92 W., Fremont County, Wind River Basin, Wyoming.

REVISED DIAGNOSIS: About 20 per cent smaller than *Grangeria canina*; length of M^{1-3} , 54 mm.; length of M_{1-3} , 55 mm. Canines greatly enlarged. Upper molars like those in *Eomoropus* except parastyle relatively larger. Lower cheek teeth similar to those of *Eomoropus* except metalophids more oblique and anterior premolars relatively larger. Mandible relatively deep, as in *Grangeria canina*.

DISCUSSION: Gazin (1956, pp. 12-15) described a new species of chalicothere from the late Uintan Badwater fauna which he referred to *Eomoropus*, under the name *E. anarsius*. The Badwater chalicothere differs from *Eomoropus amarorum* in the features listed in the diagnosis above, the most basic of which are the hypertrophied canine and deep mandible (ramus depth below M_3 to length of M_{1-3} equals 0.76, approximately as in *Grangeria canina*; in *Eomoropus amarorum* the same ratio equals 0.62). The deep mandible and greatly enlarged upper canine indicate that the lower canine in *E. anarsius* was also enlarged, as in *Grangeria canina*. Canine

hypertrophy with concomitant skull and ramus modifications is a basic feature that separates *Grangeria* from *Eomoropus*; its occurrence in *E. anarsius* indicates that this species is more properly referred to *Grangeria*. The assignment of *anarsius* to *Grangeria* is provisional, pending knowledge of the upper molars of *G. canina*.

The upper molars and posterior premolars of *Grangeria?* *anarsius* differ from those of *Eomoropus* in having larger, more anterolabially expanded parastyles. This feature may prove to be generically diagnostic of *Grangeria*. The lower cheek teeth of *G.?* *anarsius*, like those of *G. canina*, are more advanced than those of *Eomoropus amarorum* in having slightly more oblique metalophids. The anterior lower premolars are relatively larger in *G.?* *anarsius* than in *Eomoropus amarorum*, possibly owing to fringe effects of the canine growth field. The last lower molar of *G.?* *anarsius* retains a short hypoconulid, apparently a characteristic of all pre-Oligocene chalicotheres.

Grangeria? *major* (Zdansky), 1930, new combination

Eomoropus? *major* ZDANSKY, 1930, p. 66.

TYPE: Isolated M^1 or M^2 figured in Zdansky (1930, pl. 5, figs. 1-2).

HORIZON AND LOCALITY: Late Eocene beds in northern Honan, China.

DIAGNOSIS: Parastyle relatively large, as in *Grangeria?* *anarsius*. Type 20.7 mm. long and 20.8 mm. wide.

DISCUSSION: *Grangeria?* *major* is from the same locality as *Eomoropus quadridentatus*, but it is about 20 per cent larger than M^2 in that species, is more robust, and has a relatively larger parastyle (see Zdansky, 1930, pl. 5, fig. 2). The expanded parastyle suggests *Grangeria* rather than *Eomoropus*, but more knowledge of the dentition is necessary for definite generic assignment. If the type of *Grangeria?* *major* is an M^1 , it is about 35 per cent larger than that tooth in *G.?* *anarsius* and about the size of M^1 in *G. canina*. If the type is an M^2 , then *G.?* *major* is about the size of *G.?* *anarsius*.

LITOLOPHUS, NEW GENUS¹

TYPE: *Grangeria gobiensis* Colbert, 1934.

DISTRIBUTION: Late Eocene of Asia.

¹ Greek *litos*, simple, plus *loph*; in reference to the absence of a mesostyle on the molar ectolophs of this genus.

DIAGNOSIS: Medium-sized chalicotheres with low-crowned teeth. Canines slightly enlarged. P^1 present a short distance anterior to P^2 . P_1 absent. Premolars and lower molars similar to those of *Grangeria*. Upper molars like those of *Eomoropus* except lacking mesostyles; M^3 meta-
loph and posterior end of ectoloph rotated posterolabially. Mandible relatively long and slender, with a long shallow symphysis and high ascending ramus.

DISCUSSION: Colbert (1934, p. 355) assigned a new species of late Eocene chalicothere from Mongolia to *Grangeria*, under the name *G. gobiensis*, but did not discuss reasons for the generic assignment. *Grangeria gobiensis* differs from *G. canina*, the type species of *Grangeria*, in having smaller canines and a relatively longer and more slender mandible (the ratio of ramus depth below M_3 to length of M_{1-3} is about 0.56 in *G. gobiensis* and 0.75 in *G. canina*). The upper molars of *Grangeria gobiensis* differ from those of *G.?* *anarsius* (upper molars unknown for *G. canina*) in having smaller parastyles (about as in *Eomoropus*) and, more important, in totally lacking mesostyles. The absence of a mesostyle is a surprising feature to find in a late Eocene chalicothere and, together with the long slender mandible and medium-sized canines, sets *G. gobiensis* apart from species both of *Grangeria* and of *Eomoropus*. To express this relationship taxonomically, I propose making *Grangeria gobiensis* the type of a new genus, *Litolophus*.

The upper molars of *Litolophus gobiensis* appear most similar in cusp pattern to those of the older European genus *Lophiaspis*, from which they differ in being larger and relatively longer, and in having more lingually depressed paracones, more posteriorly extended protocones, and a posterolabially rotated M^3 metaloph and metacone. Knowledge of the lower dentition of *Lophiaspis* will undoubtedly reveal additional differences between it and *Litolophus*.

Premolar cusp patterns suggest that *Litolophus* is more closely related to *Grangeria* than to *Eomoropus*. The key to the relationship between *Litolophus gobiensis* and *Grangeria* lies in the unknown upper molar pattern of *G. canina*. *Grangeria canina* is so similar to the North American species *G.?* *anarsius* in comparable parts (especially the unusual degree of canine enlargement), that it seems likely that the upper molars of *G. canina*, like those of *G.?* *anarsius*, possessed mesostyles. If *Grangeria canina* should prove to lack upper molar mesostyles (which would necessitate the erection of a separate genus for *G.?* *anarsius*), the argument for generic separation of *Litolophus gobiensis* from *Grangeria* would be less strong, but would still be supported by the differences in canine enlargement and mandible proportions.

Litolophus gobiensis (Colbert), 1934, new combination

Figure 3

Grangeria gobiensis COLBERT, 1934, p. 355.

TYPE: A.M.N.H. No. 26645, crushed skull and mandible, with dentition complete except for incisors.

HYPODIGM: Type and A.M.N.H. Nos. 26644, 26646–26659; including several badly crushed skulls and mandibles, manus and pes, and caudal vertebrae.

HORIZON AND LOCALITY: Late Eocene “Irdin Manha” beds, 6 miles west of Camp Margetts, about 27 miles southwest of Iren Dabasu, Inner Mongolia.

DIAGNOSIS: Sole species of genus. Length of M^{1-3} , 67 mm.; length of M_{1-3} , 67 mm. P^2 with relatively small and posteriorly displaced protocone. M_{1-3} paralophids slightly longer than those in *Grangeria?* *anarsius*.

DISCUSSION: Colbert (1934, p. 363, fig. 4) restored *Litolophus gobiensis* as having one lower and two upper incisors on each side. After examining all available specimens of *L. gobiensis*, I do not find the evidence to support this interpretation. In the best pair of premaxillaries preserved (A.M.N.H. No. 26645), there are alveoli for at least two pairs of incisors, but the area of the median suture is too damaged to reveal whether or not a third pair had been present. The most complete symphysis (A.M.N.H. No. 26647) is considerably crushed and lacks the anterior edge. Two incisor crowns have been glued on in the area where the incisor roots should be, making it appear as if only two incisors could fit between the canines. However, if one considers the fact that the incisor roots are considerably narrower than the crowns, and that the anterior part of the symphysis is missing, there is no reason to assume that the specimen did not originally have the normal complement of three pairs of incisors. In short, I can find no evidence of incisor reduction in *L. gobiensis*.

The canines in *Litolophus gobiensis* are relatively slightly larger than those of *Eomoropus amarorum* but significantly smaller than canines in *Grangeria*. The first upper premolar (P^1) is a labiolingually compressed, single-cusped, double-rooted tooth situated slightly closer to P^2 than C^1 . The second upper premolar is like P^2 in *Grangeria canina*, differing from that tooth in *Eomoropus* in having a relatively smaller and more posteriorly displaced protocone. The third and fourth upper premolars show incipient posterior elongation of the protocone.

The lower cheek teeth of *Litolophus gobiensis* resemble those of *Grangeria* and are slightly more advanced than those of *Eomoropus* in having a better

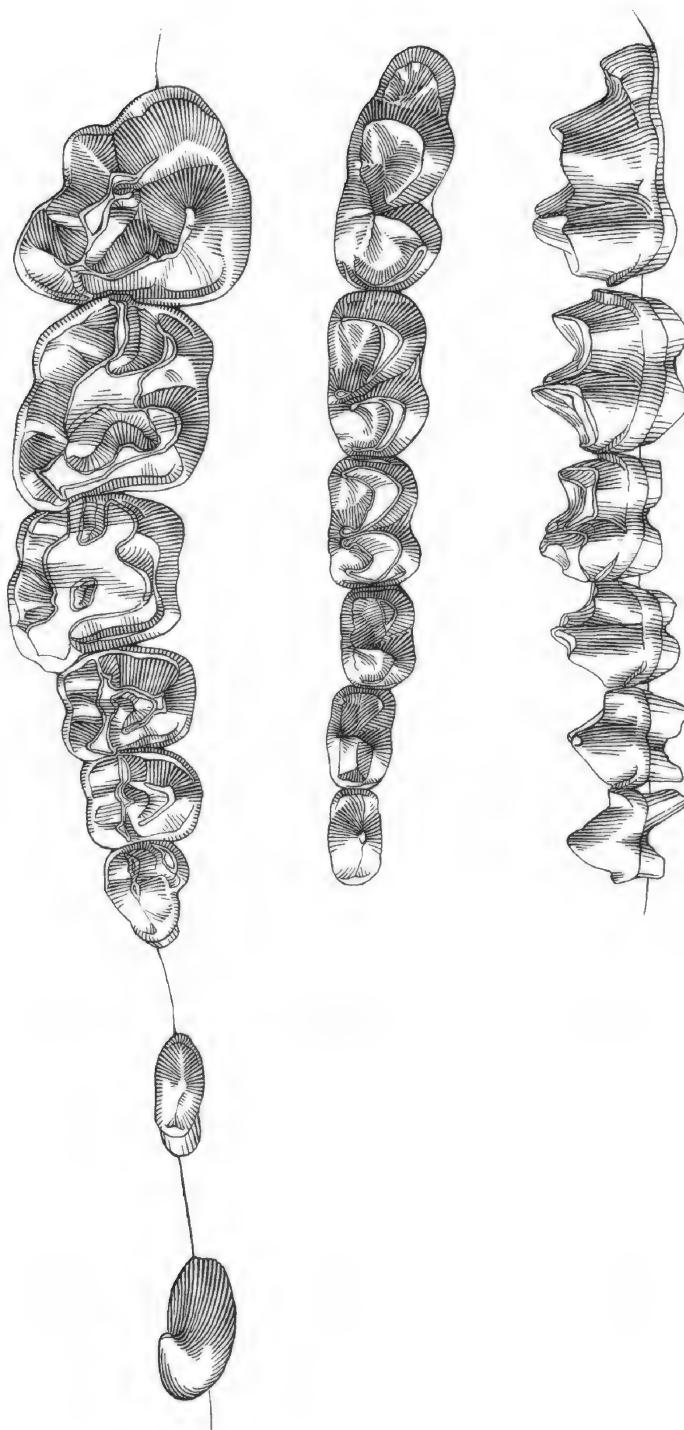


FIG. 3. *Litolophus gohensis*, new genus, type, A.M.N.H. No. 26645. *Above*: Occlusal view of upper dentition. *Below*: Occlusal and lateral views of P_2 – M_3 . From Colbert (1934). All natural size.

differentiated P_2 talonid and slightly more oblique P_3-M_3 metalophids. The M_{1-3} paralophids in *L. gobiensis* appear slightly longer than those of *Grangeria?* *anarsius*. Neither upper nor lower anterior premolars are enlarged in *Litolophus*.

The most unusual feature of the dentition of *Litolophus gobiensis* is the lack of upper molar mesostyles. The first and second upper molars are essentially like those teeth in *Eomoropus* (parastyle slightly smaller than in *G.?* *anarsius*), except that the paracone is more convex and slightly less lingually depressed, and there is no trace of a mesostyle. The last upper molar further differs from that tooth in *Eomoropus* in having the metaloph and posterior end of the ectoloph rotated posterolabially, so that the metaloph is almost in line with the main part of the ectoloph and the posterior ectoloph segment trends posterolabially, instead of posteriorly. In addition, M^{1-3} protocones appear to be more posteriorly extended (an advanced condition) in *Litolophus* than in *Eomoropus* or *Grangeria?* *anarsius*.

The absence of molar mesostyles in *Litolophus* is difficult to explain, since the lower molars have oblique metalophids. However, despite the differences in upper molar cusp patterns, molar occlusion in *Litolophus* was not much different from that in *Grangeria* and *Eomoropus*. In these latter two genera, paracone depression and mesostyle enlargement are not far advanced, and the metalophids are low and not completely oblique, so that molar occlusion still consisted largely of shear between the anterior sides of the protolophs and metalophs above and the posterior sides of the protolophids and hypolophids, respectively, below. It was not until the Oligocene (in *Schizotherium*) that the upper molar ectolophs became prominent enough to play a dominant role in chalicotherid molar occlusion.

The available skulls of *Litolophus gobiensis* (A.M.N.H. Nos. 26644, 26645, and 26646) are too badly crushed to allow extensive comparison with those of other genera. Colbert's (1934, p. 359, fig. 1) side view restoration, showing a relatively long, low skull, with about equal preorbital and postorbital portions and with prominent sagittal and lambdoidal crests, is probably reasonably accurate. A.M.N.H. No. 26645 shows a separate foramen ovale and a short alisphenoid canal, but the ear region is too damaged to allow interpretation of the tympanic and entotympanic.

The mandible of *Litolophus gobiensis* is relatively long and slender, differing from that of *Eomoropus* in having the condyle situated higher above the tooth row, and in having a more broadly convex and more ventrally but less posteriorly extended angular process.

Colbert (1934, pp. 364-365, including fig. 5, and pp. 368-371, including fig. 6) described and figured the manus and pes of *Litolophus gobiensis*. The carpus is similar to that of *Eomoropus amarorum*, except that it is slightly wider and has a more extensive lunar-magnum contact, as would be expected in a heavier animal. The tarsus is also similar to that of *E. amarorum*, except that the astragalus has a slightly longer, more anteriorly extended cuboid facet, with the astragalus-cuboid contact visible in anterior view. The navicular in A.M.N.H. No. 26656, illustrated in Colbert's figure 6, has been restored as too high (proximodistally); it actually is as relatively low and wide as the navicular in *Eomoropus amarorum*. The entocuneiform, which is apparently oriented upside down in Colbert's figure 6, is slightly longer than that of *Eomoropus amarorum*, and has a prominent distal facet for the vestigial first metatarsal (see Radinsky, 1963b).

The metapodials of *Litolophus gobiensis* have equal-sized, evenly convex, sesamoidal and phalangeal facets, as in *Eomoropus* and other Eocene perissodactyls, and do not display the specializations seen in metapodials of later chalicotheres (*contra* Colbert, 1934, p. 368). The metatarsals of *L. gobiensis* are slightly longer than the metacarpals; in post-Eocene chalicotheres the opposite is true. The proximal phalanges are similar to those of other Eocene perissodactyls and lack the oblique proximal facets and long, deeply grooved, distal facets seen in *Moropus*. The second phalanges are relatively short and deep and have a long, convex, grooved, distal articular facet, which extends up to the middle of the anterior face. This fact suggests that the terminal phalanges in *Litolophus* (none of which are preserved) were relatively deep and narrow and possibly bore claws. In any case, the digits appear to have been held fairly straight, as in most other perissodactyls, and not strongly flexed, as in later chalicotheres.

Litolophus? *ulterior* (Chow), 1962, new combination

Eomoropus ulterior Chow, 1962, p. 219.

TYPE: G.M.P. No. VM0053, lower cheek tooth row, with P_2-M_3 . (Figured in Chow, 1962, p. 220, fig. 1.)

HORIZON AND LOCALITY: Late Eocene or early Oligocene beds at Hsiaoshaho, eastern Yunnan, China.

REVISED DIAGNOSIS: About 17 per cent smaller than *Litolophus gobiensis*. Length of M_{1-3} , 55.5 mm.; length of P_{2-4} , 28 mm.

DISCUSSION: *Eomoropus ulterior*, known only from the type, differs from *E. amarorum* and *E. quadridentatus* in having a relatively shorter premolar series. In *E. ulterior* the ratio of the length of P_{2-4} to the length of M_{1-3}

equals 0.50; in *E. amarorum* the same ratio equals 0.62. Another difference that seems apparent from Chow's illustration is that the molar metalophids are slightly more oblique in *E. ulterior* than are those in the other species of *Eomoropus*. In this latter feature *E. ulterior* resembles species of *Grangeria* or *Litolophus*. In *Grangeria?* *anarsius* the lower premolar series (total length unknown for *G. canina*) is slightly relatively longer than that in *Eomoropus amarorum* and significantly relatively longer than that in *E. ulterior*. However, in *Litolophus gobiensis* the ratio of the length of P_{2-4} to the length of M_{1-3} averages about 0.55, close to that of *E. ulterior*. *Eomoropus ulterior* is about 17 per cent smaller than *Litolophus gobiensis*, but from Chow's illustration I can see no important differences in cusp pattern between the two species. Thus, on the basis of available evidence, it appears that *Eomoropus ulterior* is more properly assigned to *Litolophus* than to *Eomoropus*. Knowledge of the upper dentition of *E. ulterior* is necessary for conclusive proof of its affinities.

? CHALICOTHERIOIDEA

Lunania youngi Chow, 1957

Chow (1962, p. 224) suggests that *Lunania youngi*, first described by Chow in 1957 as a tapiroid, is probably a chalicotherere. *Lunania youngi* is known only from a lower jaw fragment, with M_{2-3} , from late Eocene beds in the Lunan Basin, Yunnan, China. From Chow's (1962, p. 220, fig. 1) illustration the M_{2-3} appear to have oblique metalophids and a cusp pattern generally similar to that of *Eomoropus* (but lacking metastylids). *Lunania youngi* is about 40 per cent smaller than *Eomoropus quadridentatus* and, if it actually represents a diminutive line of chalicotheres, may be related to *Eomoropus?* *minor*. The latter species is known from an isolated upper molar from northern Honan, China, and is about 40 per cent smaller than M^1 of *Eomoropus quadridentatus*.

PERISSODACTYLA, SUPERFAMILY *INCERTAE SEDIS*

Schizotheriodes parvus Hough, 1955

Hough (1955, p. 34) proposed a new genus and species, *Schizotheriodes parvus*, for two upper molars, M^{2-3} (U.S.N.M. No. 20205), from the late Eocene Sage Creek fauna of southwestern Montana. Hough referred *Schizotheriodes* questionably to the Chalicotherioidea mainly on the basis of the large M^3 parastyle (which, however, is more compressed antero-lingually-posterolabially than are chalicotherere parastyles). The only

other features at all suggestive of chalicotheriid affinities are a slight swelling midway down the posterior side of the worn M^2 protoloph, and, also on M^2 , a sharp cingular cuspule between the paracone and metacone (which is probably merely an abnormal variation, but may indicate incipient mesostyle development).

The absence of a distinct protoconule is a strong argument against placing *Schizotheriodes* in the Chalicotherioidea. Except for the large para-style and the minor features described above, the molar cusp pattern of *Schizotheriodes* resembles that of the Tapiroidea, with high, uninterrupted, transverse lophs and a convex, unlengthened metacone. However, in view of the limited and contradictory evidence now available as to its affinities, it seems best for the present to postpone definite generic assignment of *Schizotheriodes*, and to leave it *Perissodactyla incertae sedis*.

PHYLOGENY

The dentition of the earliest Eocene genus *Paleomoropus*, while already definitely chalicotherioid, bridges the gap between that of the undifferentiated perissodactyl stock and the dentition of the more specialized later chalicotheres. The early to middle Eocene European genus *Lophiaspis* probably arose from a form similar to *Paleomoropus* and, if it still retains the first upper premolar, represents a morphological type from which all later chalicotheres may be derived. By late Eocene time chalicotheres had radiated into at least three lines: the Asiatic genus *Litolophus*, representing a persistently primitive stock which never developed molar mesostyles; *Eomoropus*, known from North America and Asia, representative of the main line of chalicothere evolution; and *Grangereria*, known from Asia and probably also North America, a specialized offshoot from *Eomoropus* which developed greatly enlarged canines. *Lunania*, a poorly known Asiatic genus, may represent a late Eocene line of diminutive chalicotheres. *Eomoropus* provides a suitable morphological type for the ancestry of Oligocene and later chalicotheres.

The dearth of chalicotheres in the well-known western North American Oligocene faunas suggests that the eomoropid-chalicotheriid transition took place elsewhere. Oligocene chalicotheriids (species of *Schizotherium*) are known from Europe and Asia, but only on the latter continent is *Eomoropus* also present in late Eocene faunas. Thus from the available evidence it appears that chalicotheriids arose in Asia at the end of the Eocene, spread to Europe in the Oligocene but did not reach North America until the Miocene.

EVOLUTION OF CHALICOTHEROID DENTITION

The earliest representatives of the various perissodactyl superfamilies appear to have been extremely similar in skeletal morphology, and the differences that initiated the basic radiation of the order are obvious only in the dentition. The molar pattern of *Paleomoropus*, the oldest known chalicotherere, may be derived from that of the stem perissodactyl (which was probably similar to *Hyracotherium angustidens*), by enlargement of the parastyle and fusion of the metaconule and hypocone into a high, uninterrupted, shearing loph (undoubtedly with concomitant development of a high hypolophid below); the protoconule remained distinct on the anterior cross crest. This upper molar cusp pattern, characterized by an interrupted anterior transverse crest and a high, continuous, posterior cross crest, is the feature that set chalicotheres apart from all other perissodactyls. Functionally it combines aspects of molar occlusion of both hippomorphs (*sensu stricto*) and ceratomorphs. The high metaloph allows continuous transverse shear against the posterior side of the hypolophid, as in tapiroids and rhinocerotoids, while on the protoloph the bulge of the protoconule interrupts transverse shear, as in equoids, adding an element of crushing to the shear. Enlargement of the parastyle lengthens the area available for transverse shear between the anterior side of the protoloph (continuous lingually only to the protoconule) above and the posterior side of the protolophid below.

The transition from the molar pattern of *Paleomoropus* to that of *Lophiaspis* involved an increase in height of crests, posterior deflection of the protoconule, and posterior extension of the protocone. The higher, more acute lophs increase the efficiency of transverse shear. Posterior deflection of the protoconule provides a straighter anterior protoloph face for shear against the protolophid, and also allows a more continuous shear lingually toward the protocone. Posterior extension of the protocone provides a buttress against which food could be crushed by the anterolingual face of the lingually sweeping hypoconid.

The upper molars of the late Eocene Asiatic chalicotherere *Litolophus* are essentially like those of *Lophiaspis*, and occlusal relationships appear to have been basically the same. Prominent metastylids on the lower molars of *Litolophus* and other late Eocene chalicotheres (probably present also in the earlier forms) sheared against the anterior faces of the protoconules, which are more posteriorly situated than the protoconules.

The upper molars of the late Eocene genera *Eomoropus* and *Grangeria* are advanced over those of *Lophiaspis* and *Litolophus* by the presence of a mesostyle, developed by outward buckling of the ectoloph between the

paracone and metacone and the lingual depression of the paracone. This increases the length of ectoloph available for vertical shear, providing a posterolabially oriented segment (from paracone apex to mesostyle) to shear vertically against the lingual side of the oblique metalophid below. It also brings the anterior edge of the paracone into line with the labial end of the protoloph for vertical shear (grading lingually into transverse shear) against the posterior side of the protolophid. However, the mesostyles in *Eomoropus* and *Grangeria* are small enough so that molar occlusion was probably not very different from that in the contemporaneous mesostyle-less genus *Litolophus*, with shear along transverse crests still about as important as vertical ectoloph shear. *Grangeria* differs from *Eomoropus* mainly in having greatly enlarged upper and lower canines, a specialization which removes *Grangeria* from the main line of chalicotheriid evolution.

The transition from the dentition of *Eomoropus* to that of the Oligocene and later chalicotheriids involved several modifications which essentially carry to an extreme trends initiated in *Eomoropus*. The upper molars became relatively longer and are dominated by the ectolophs, which were transformed into high, W-shaped, shearing ridges by enlargement of the mesostyle, further lingual displacement of the paracone, and fusion of the parastyle with the anterior edge of the paracone into a continuous shearing ridge. Together with these changes, the metalophids became higher and more lingually (more obliquely) directed, for vertical shear against the paracone-mesostyle segment of the ectoloph. The protoloph was shortened by the extreme posterior displacement of the protocone, which left only the labial half (protoconule) for shearing against the protolophid below. The posteriorly displaced protocone became a relatively large, almost isolated, bluntly conical cusp, as in titanotheres. The last lower molar lost its hypoconulid. As a result of these changes, vertical ectoloph shear became by far the most important occlusal action, and transverse shear along the cross crests was reduced to insignificance. The enlarged rounded protocone assumed increased importance for crushing food against the hypoconid.

In the anterior dentition of advanced chalicotheres the upper incisors, canine, and first premolar were lost, and the lower canine was reduced or lost. With the exception of the last lower premolar, the premolars remained submolariform (P^2-4 with only one lingual cusp), and the premolar series became increasingly short relative to the molar series. All the dental changes described above were accomplished by Oligocene time, for the end results are seen in the oldest chalicotheriid, *Schizotherium*. Besides the changes in dentition, radical modifications in foot structure trans-

formed the typical perissodactyl feet of *Eomoropus* into the sharply flexed and extended, grotesquely clawed feet of the chalicotheriids. The differences between the primitive Eocene chalicotheres, including the most advanced Eocene genus, *Eomoropus*, and the later, aberrantly specialized chalicotheres, seem basic enough to justify division of the superfamily into two families, the Eomoropidae and the Chalicotheriidae.

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